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THE
AMERICAN NATURALIST

VOL. XLIX. *July, 1915* NO. 583

THE RÔLE OF THE ENVIRONMENT IN THE REALIZATION OF A SEX-LINKED MENDELIAN CHARACTER IN DROSOPHILA

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INTRODUCTION

THE mutant, from which the stock with "abnormal abdomen" was derived, appeared in 1910. It is characterized by a peculiar condition of the pigment bands and segments of the abdomen as shown in Fig. 1. The range of variation of the character is very great; in its most

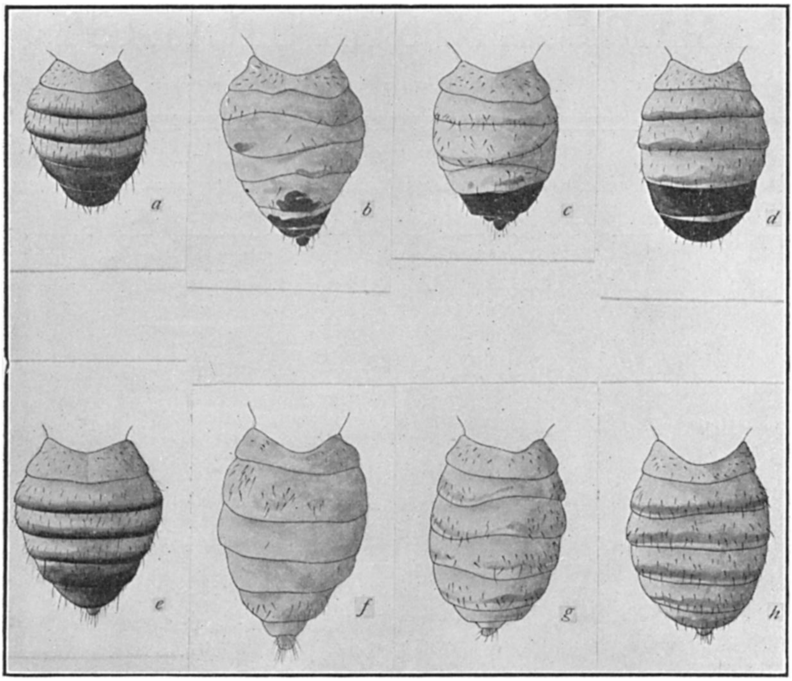

FIG. 1.

extreme condition not only do the pigment bands totally disappear, but even the lines between the metameres are broken up, and the location of the external genitalia may be shifted to a more terminal position. All stages exist between this extreme modification and a condition that can not be distinguished from the normal. Owing to this wide range of variability the study of the inheritance was very difficult until it was found that the realization of the type is a function of the environment.

In the more extreme types the abdomen is deformed to such an extent that copulation is difficult or impossible. The sterility caused in this way helped also to make the work burdensome, especially when breeding was made with pairs. Instead of pairs, cultures of ten to twenty individuals of the more extreme type were resorted to, as a rule insuring the successful mating of some individuals. Aside from this mechanical difficulty in mating, the mutant race is quite vigorous and of good size.

Two principal obstacles delayed the formation of a pure strain. The new character is a sex-linked dominant,[1] but both the heterozygous and the homozygous condition overlap the normal type which makes the selection of pure females difficult. Any male, however, that shows abnormal abdomen at all is pure, for the character is borne by the X chromosomes of which he has but one.

The other obstacle was what at first appeared to be a perpetual reversion of stock, seemingly pure, to the normal. So constantly did this occur, that, for some time, I thought that I had an ''ever-sporting'' variety—one that reverted to the normal without apparent provocation. I found, however, that the first flies that hatched in the best-fed cultures were entirely abnormal, while those that emerged later were less abnormal, until finally those that emerged when the cultures were nearly at an end were invariably normal flies. It seemed at first possible that such stock might be impure, and that the abnormal flies hatched sooner than the normal, but this view was negatived by the fact that normals hatch as soon as do the abnormal flies.

The one remaining possibility seemed to be that development of the abnormal abdomen depended on some definite condition of the culture—one that was present when the food was fresh and the bottle wet, but which disappeared as the food was used up and the bottle got dry. I tested this hypothesis in many ways. Stock was used that had been pure for nine generations. As a bottle dried up an ever increasing proportion of normal flies appeared. At intervals lots of flies were taken out and put into new bottles where they were abundantly fed. Their first progeny, as recorded below, shows that under the new conditions the offspring were sometimes extremely abnormal irrespective of the general condition of the original stock when used.

[1] Morgan, T. H., ''A Dominant Sex-Linked Character,'' *Proceed. Soc. Exp. Biol. and Medicine,* IX, October 18, 1911.

	Condition of Parents	Next Generation
Feb. 26.	Most flies abnormal—a few were normal	Very abnormal.
Feb. 27.	More than half were normal	Flies fairly normal.
Feb. 28.	About half were normal	Nearly all abnormal.
Feb. 29.	Practically normal	Very abnormal.
Mch. 1.	Nearly all normal	Abnormal, a few normal.
Mch. 4.	Normal	Very abnormal.
Mch. 5.	Normal.	Very abnormal.

The preceding case shows that there is no necessary relation between the development of the abnormality in the parent and that in the offspring. This is only a sample of a large amount of similar data. But this evidence does not show what special conditions make for abnormality. In order to study this problem I generally used heterozygous females which were obtained either by mating an abnormal male to a wild (virgin) female (in which case the daughters will be abnormal under suitable conditions and the sons normal), or reciprocally by mating a normal male to an abnormal female (when all the daughters will be abnormal (heterozygous) and all the sons pure abnormal). Many experiments had shown that the heterozygous female changes over more promptly to the normal character than does the homozygous male and the latter sooner than the homozygous female.

The one outstanding fact for some time was that as a bottle crowded with flies gets old there is always a change from day to day from abnormal towards normal, but it remained to be shown whether the change was due to the drying out of the culture, or to any one of a dozen other parallel changes that obviously are going on at the same time. The more significant results of a prolonged set of experiments may be summed up as follows:

1. *Starvation.*—Lack of food does not bring about the change from abnormal to normal. Flies that are so starved as to be extremely small may be very abnormal.

2. *Acid, Alkali or Neutral Condition of Food Stuff.*—Most cultures change in the course of the ten to twelve days from an acid through a neutral to an alkaline condition. Fresh fermenting banana (in the old and acid

medium) was made more acid (and liquid) by adding an equal amount of a 5 per cent. solution of acetic acid. Other food was made alkaline by adding dry sodium bicarbonate, or a 1 per cent. solution of sodium hydroxide. The acid food gave very abnormal flies; the alkaline food was difficult to control as the flies refused in most cases to lay eggs on it, if it remained alkaline, and the food often dried up, or putrified, or grew mouldy. Moreover, the highly alkaline food often became acid over night owing to fermentation changes taking place within the pieces of fruit used for food. But several times good results were obtained with cultures that had been strictly neutral and often alkaline throughout the time of the experiment and from these the flies were abnormal. Omitting all details it may be stated that an acid or alkaline (neutral) condition as such is not the cause that conditions the character.

3. *Food of Parents.*—At one time it seemed possible that the kind of food that the female was supplied with might for a time continue to affect her eggs, even although the parent was transferred to a medium that acted in the opposite direction. Careful tests showed conclusively that such was not the case. Some of the evidence for this statement will be given later.

4. *Egg versus Sperm.*—Heterozygous females may be produced either by using a normal female and abnormal male, or conversely an abnormal female and a normal male. Certain cultures seemed, at one time, to show that when the egg parent was abnormal the offspring were more abnormal than when the egg parent was normal, but careful tests disproved this view. The difference in the cultures, that led to the suspicion mentioned, was due to the large number of eggs laid by the normal females, hence greater crowding and more rapid disappearance of the moist food.

5. *Influence of Genetic Factors.*—Certain mutant stocks, notably black, seemed at times to show the abnormality less strongly than other stocks, but here, as in the last

case, the results were found to be due, when carefully tested, to the number of eggs laid and the promptitude with which they are laid when the food is fresh. The question will again come up in certain of the crosses.

6. *Amount of Water in Food.*—Normal cultures lose much of their water as the brood of flies develops. It was a fact noticed at the start that in "wet" bottles the abnormal characters appeared to best advantage, and in most of the work on linkage that knowledge was utilized. But whether the wetness was only incidental to other changes, or in itself the normal condition was not precisely determined. Under all conditions the air in the bottles must be completely saturated with moisture so that we must be dealing with the water taken in with the food and not with the amount of water in the inspired air. In three ways the effect of water was studied. (1) Food that had been fermenting for two or three days in the old acid medium was squeezed until freed of much of its water. The solid part was then further dried superficially by pressing between pieces of filter paper, and finally put into a bottle with more dry filter paper. The fluid squeezed out was diluted with an equal amount of water, and put into another bottle. Virgin normal flies and abnormal males of pure stock were set free in these two bottles. The results at the end of nine days were most striking. In the dry bottles the F_1 females were all normal; in the wet bottles the F_1 females were extremely abnormal.

7. *Changing the Adult from Wet to Dry and Vice Versa.*—In this same series the old (P_1) flies that had been in the wet bottle were transferred to dry food, and conversely the "dry" flies to wet food. Their progeny showed the influence of the food that they were reared upon, and no effect of the feeding in the previous bottle. Once more they were changed, the wet to dry, the dry to wet, and the results were the same as before, *i. e.,* the actual conditions, not the preceding ones, fully accounted for the results that were obtained.

8. A culture that was giving F_1 normal females (that were heterozygous for abnormal) was made extremely wet; into a sort of swamp. The flies that emerged during the next six days were normal, on the seventh day the flies were slightly to fairly abnormal, on the eighth and ninth days the flies that emerged were slightly to quite abnormal. It is evident that the influence of the wet conditions does not appear unless the flies are subjected to it throughout most of the larval life, or else that the first few days of larval life is the critical period.

9. Larvæ that were about ready to pupate were transferred to very wet new food, where they pupated, in from 12 to 24 hours. The pupæ remained in the same bottles until the flies emerged. These flies were entirely normal in appearance; the stock from which the larvæ came were also giving rise to normal flies. The sojourn of one or two or even three days in a wet environment at the end of the larval life does not suffice to alter the effects that have already been induced in an earlier stage.

Conclusions.—The preceding evidence makes clear that the amount of water in the food, determines the realization of the "abnormal" type. The water may produce its effect either by being taken in with the food, or by being directly absorbed; or it may determine the nature of the bacterial or yeast flora that in turn determines the nature of the fermentative changes that take place within or without the larvæ. It would be a very difficult matter to find out in which one of these ways the effects are brought about. However this may be, it is possible for the experimenter to determine at will the nature of the flies that will be produced in his cultures by controlling the food supply.

THE LINKAGE OF THE FACTOR FOR ABNORMAL ABDOMEN WITH OTHER SEX-LINKED FACTORS

Owing to the overlapping of the abnormal and normal types, the study of the linkage has presented unusual difficulties. The following experiments were made for the most part during the second year when the influence of the environment was not fully under control. The conditions under which the experiments were made were, however, favorable for the appearance of the abnormal condition, at least in the first counts of each brood, for the bottles were supplied with an abundance of wet fermented food.

The linkage of abnormal abdomen with white eyes and yellow body color was studied in different combinations; and since the factor for abnormal abdomen proved to be quite near the other two factors the choice was a favorable one in certain respects. A special method by means of which the error, due to the variability of the character, can be largely eliminated will be given after the evidence has been presented.

The Linkage of Abnormal and White

When red-eyed (R) abnormal (Ab) females were mated to white-eyed (W) normal (N) males, red abnormal males and females were produced.[2] When these were mated the results recorded in the next table were obtained.

By means of the following diagram, I have tried to show what the expectation is for this combination. The two parallel lines are intended to represent the two sex chromosomes of the F_1 female. From her mother she

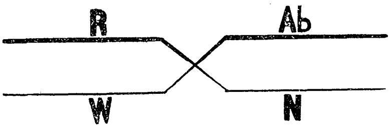

Diagram I.

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[2] Throughout this paper I have used the letters R for red eyes, W for white-eyes, N for normal abdomen, Ab for abnormal abdomen, Y for yellow, B for black instead of using the allelomorphic system; because for present purposes, where analyses are unnecessary, these letters suffice most simply to indicate the operations that are involved. For comparison with other papers the allelomorphic symbols for the same characters would be:

w = the factor for white. W = its normal allelomorph = red.
A'b = the factor for abn. abd. a'b = its normal allelomorph = normal abd.
y = the factor for yellow. Y = its normal allelomorph = gray.
b = the factor for black. B = its normal allelomorph = gray.

got the sex chromosome bearing the factors for red and abnormal (RAb), from her father the homologous sex chromosome that carries the factors for white and normal (WN).

TABLE I

PARENTS: RAb ♀ BY WN ♂

F_1: RAb ♀—RAb ♂

RAb		WN		RN		WAb		No. of Culture
♂	♀	♂	♀	♂	♀	♂	♀	
157	336	157	......	9	2	5	......	II$_1$
143	266	154	......	6	1	3	......	II$_4$
106	362	130	......	2	3	1	......	II$_5$
88	151	62	......	4	......	2	1	II$_{16}$
95	200	100	......	2	......	1	......	II$_{20}$a
24	68	41	......	2	......	......	......	II$_{28}$
34	64	20	......	......	1	1	......	II$_{29}$
647	1,447	664	......	25	7	13	1[3]	

If these chromosomes unite at synapsis without exchange of materials, half of the eggs that result (one chromosome being eliminated in the polar bodies) will contain the red normal combination, the other half the white normal. These represent the "non-cross-over" gametes. If, however, these chromosomes should cross and reunite, as in the diagram (the crossed lines indicate where the crossing over may occur, not how it occurs), the two resulting chromosomes will be red-normal RN, and white abnormal, WAb, which represent the other (the cross-over) kinds of gametes of the F_1 female. The ratio in which they are produced is the gametic ratio and is a measure of the linkage.

In the F_1 males there is but one X chromosome, hence there is no opportunity for interchange here between the X chromosomes. The mate of the X chromosome is, in the male, the Y chromosome. Other experiments have shown that the Y chromosome carries no factors; hence interchange seems precluded; and, so far, no loss of X chromosome factors to the Y chromosome has ever been observed. The X chromosome passes into the female-producing spermatozoon, which carries therefore an X chromosome received from the mother of the F_1 males and bears her character. In the present case the male carries the chromosome bearing red abnormal.

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[3] An unexpected individual that can be accounted for by equational nondisjunction.

Since red and abnormal dominate, all the F_2 females should be red abnormal, except in so far as the conditions suppress the abnormal and induce the normal type. The experiment, Table I, shows that very few normal females were present.

Four classes of males are expected—the large class of non-cross-overs RAb and WN, and two small classes of cross-overs RN and WAb. It will be observed (Table I) that the linkage between R and Ab is very strong, since nearly all of the males are either RAb (647) or NW (664). Only a few crossovers RN (25) and WAb (13) males were present. The percentage of crossing over is 1.97 per cent. when the abnormal males alone are used for calculation.

In the reciprocal cross the RAb male was mated to WN female, and gave in F_1 RAb females and WN males. The F_2 record is given in Table II.

TABLE II

Parents: RAb ♂ by WN ♀

F_1: RAb ♀—WN ♂

RAb		WN		RN		WAb		
♂	♀	♂	♀	♂	♀	♂	♀	
68	62	59	47	1	0	2	1	II_{2}
38	55	69	68	0	3	0	1	II_{20}
115	170	130	147	2	2	2	2	II_{21}
103	103	97	103	3	7	4	2	II_{22}
75	96	94	49	2	1	5	0	I_{13}
399	486	449	194	8	13	13	6	

Since the same two pairs of factors enter as before, the same chromosome diagram will suffice for the gametes of the F_1 female. The F_1 male is, however, a double recessive (WN); in consequence four classes of females are expected as well as of males. The gametes of the F_1 female are as before the following:

Non-cross-over	RAb	Crossover	RN
gametes	WN	gametes	WAb

The percentage of crossing over as calculated from the abnormal classes (males and females) is 2.1.

In order to obtain further data for linkage the preceding experiment was repeated in the winter of 1914, but the linked factors entered differently combined. The experiment was begun by crossing white abnormal females to wild males which gave red abnormal females and white abnormal males. These were inbred and gave the following results in five different cultures (kept with abundance of moist food).

TABLE III

PARENTS: WAb ♀ BY RN ♂

F_1: RAb ♀—WAb ♂

No.	RAb		WN		RN		WAb	
	♂	♀	♂	♀	♂	♀	♂	♀
1	0	44	0	2	33	0	52	55
2	4	66	0	0	57	4	57	50
3	1	38	0	0	62	0	37	48
4	1	111	7	1	95	0	77	100
5	1	65	2	0	65	0	28	34
Total	7	324	9	3	312	4	251	287

The sum of the two non-cross-over males (251 + 312 = 563) plus the cross-overs (16) divided into the sum of the cross-over males (7 + 9 = 16) gives 2.7 as the percentage of crossing over. Since the white normal males may receive contributions from the changed white abnormal, the result may be freer from error if the two correlative abnormal male classes, viz., red abnormal (7) and white abnormal (251), be utilized to calculate crossing over. Dividing the former by the total (251 + 7) gives 2.7 per cent. of crossing over which is the same as the preceding estimate.

The reciprocal cross, RN ♀ by WAb ♂, was also made once and the results in F_2 combined with other similar results are as follows:

RN		WAb	RAb		WN
♂	♀	♂	♂	♀	♂
1,220	(with RAb)	854	20	1,323	89

The other results were obtained in the following way: The abnormal red eyed F_2 females obtained from the first experiment are heterozygous for abnormal (AbN) and white (RW), except in so far as this class may contain cross-over flies that are heterozygous in white but homozygous in abnormal AbWAbR. Except for these flies, these F_2 females are like the F_1 females, and if mated to abnormal white males will continue in each successive generation to give the same linkage data as do the F_2 classes above. If bred in pairs exceptional females homozygous for abnormal will be at once detected, and can be thrown out; but even if bred in small batches of four or five females the chance is small of including homozygous abnormal females.

In these counts no separation of the normal red females (when they occurred) from the abnormal red females was made but the red females were put into the latter class. Since the females were not intended to be used for comparison this grouping does not affect the problem involved. If we divide the cross-over red abnormal males (20) by the abnormal white males (854) plus 20 abnormal red males, we get the per cent. of cross-overs which is here 2.3. This is slightly lower than that obtained for the preceding data.

Black, Red, Abnormal by Gray, White, Normal

Another series of experiments, carried on for a somewhat different purpose, may be utilized here for further data. Gray, white, normal females were mated to black, red, abnormal males. The daughters were gray, red, normal (or slightly abnormal), and the sons gray, white, normal. Inbred they give the results shown in Table IV. Since the factor for black is not sex-linked, the gray and the black classes may be added together as shown in Table V.

The results differ from those of Table II in the following points: There are relatively more red normals which may be assumed to be due to the external condition pre-

TABLE IV

PARENTS: BRAb ♂ BY GWN ♀

F$_1$: GRN OR SLIGHTLY Ab ♀—GWN ♂

GRAb		BRAb		GWN		BWN		GRN		BRN		GWAb		
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
35	52	7	8	160	179	48	58	126	146	54	43	...	...	III$_{5}$
50	78	6	16	111	104	34	18	48	30	34	28	...	...	III$_{29}$
65	52	0	1	221	187	13	7	131	159	11	16	1	...	III$_{35}$
187	152	27	36	254	268	58	72	102	99	45	65	4	1	III$_{48}$
33	56	12	12	37	63	15	10	0	0	0	0	...	...	III$_{49}$
103	140	34	34	146	191	52	42	54	52	21	14	6	1	III$_{50}$
50	33	14	10	93	69	22	24	30	24	7	6	1	...	III$_{52}$
8	71	0	2	76	123	20	40	80	66	27	61	...	...	III$_{59}$
91	74	17	16	89	89	30	45	75	66	79	59	1	...	III$_{69}$
92	88	27	24	135	153	33	59	62	76	19	20	...	1	III$_{89}$
2	8	6	3	7	8	3	3	0	0	0	0	...	...	Ex.
82	95	32	23	195	191	47	65	66	94	34	29	...	1	III$_{19}$
798	899	182	185	1,524	1,625	375	443	774	812	331	341	13	4	

vailing at the time, or else the black factor may have had some influence that is favorable to the normal condition in the heterozygous abnormal flies. If the latter were the true explanation we can understand the large number (here) of the GRN class (for two thirds are heterozygous in black and intermediate in color) and the complete absence of the BWAb class which should be one third as frequent as the GWAb class. A special examination was made to test this possibility and will be described

TABLE V

PARENTS: BRAb ♂ BY GWN ♀

F$_1$: GRN OR SLIGHTLY Ab ♀—GWN ♂

RAb		WN		RN		WAb		
♂	♀	♂	♀	♂	♀	♂	♀	
42	60	208	237	179	189	......	......	III$_{5}$
56	94	145	122	82	58	......	......	III$_{29}$
65	53	234	194	142	175	1	......	III$_{35}$
214	188	312	340	148	164	4	1	III$_{48}$
45	68	52	73	......	......	......	......	III$_{49}$
137	192	198	233	75	66	6	1	III$_{50}$
64	43	115	93	37	30	1	......	III$_{52}$
8	73	96	163	107	127	......	......	III$_{59}$
108	90	119	134	154	125	1	......	III$_{69}$
119	112	168	212	81	96	......	1	III$_{89}$
8	11	10	11	......	......	......	......	Extra
105	118	242	256	100	123	......	1	III$_{15}$
841	1,102	1,899	2,068	1,105	1,153	13	4	

later, but it may be stated beforehand that no certain evidence could be found in favor of this view. The number of larvæ in a culture brings about a rapid alteration in the condition of the food, so that it changes more quicky from an acid to a neutral or alkaline condition. If the black flies used gave vigorous F_1 offspring the effect in question could be explained as due to numbers, and not as connected with the black factor.

Gray, Red, Abnormal by Black, White, Normal

The results of this cross and of its reciprocal are given in Tables VI and VII. The RN class (cross-over) is relatively too large, but the increase is due to the transition from abnormal to normal.

TABLE VI

Parents: GRAb ♀ by BWN ♂

F_1: GRAb ♀—GRAb ♂

GRAb		BWN		GWN		BRAb		GRN		BWAb		GWAb		BRN	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
95	194	49	2	163	1	20	32	56	71	...	...	4	.....	24	45

Parents: BWN ♀ by GRAb ♂

F_1: GRAb ♂—GWN ♀

GRAb		BWN		GWN		BRAb		GRN		BWAb		GWAb		BRN	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
215	143	91	91	314	276	56	11	28	170	...	...	9	2	41	59

THE LINKAGE OF ABNORMAL, YELLOW, AND WHITE

In the following crosses three pairs of sex-linked factors characters are involved, viz., yellow, white, abnormal and their normal allelomorphs whose location at one end of the X chromosome is shown in Diagram II.

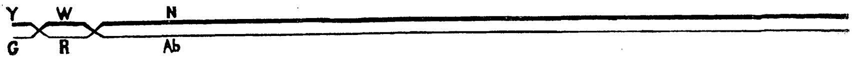

Diagram II.

Gray, Red, Abnormal by Yellow, White, Normal

When a YWN ♀ is crossed to a GRAb ♂ the daughters are GRAb and the sons YWN. The F_1 male is a triple recessive, hence, neither his female-producing nor his male-producing sperm affect the dominant characters that the eggs carry, and in consequence the entire F_2 count, females as well as males, are indicators of the gametic composition of the eggs of the F_1 female. The F_2 results are given in Table VII.

TABLE VII

PARENTS: GRAb ♂ BY YWN ♀

F_1: GRAb ♀—YWN ♂

	YWN		GRAb		YRAb		GWN		YWAb		GRN		YRN		GWAb		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
1	45	59	44	51	...	...	...	...	...	...	6	3	...	...	...	...	I_1
2	83	69	59	53	...	...	...	...	...	...	19	31	...	...	...	...	I_5
3	115	107	132	150	1	2	...	...	6	5	4	7	...	...	...	...	I_7
4	174	177	152	205	...	2	5	2	4	...	6	9	...	1	...	...	I_{10}
5	100	128	108	150	...	7	1	2	5	3	2	9	...	...	...	...	I_{11}
6	42	52	58	40	...	2	1	2	3	...	1	1	...	...	...	...	II_3
7	92	94	105	114	...	17	1	1	1	1	12	...	...	1	...	...	II_6
8	105	130	123	97	...	...	2	4	1	...	3	4	...	3	...	...	II_8
9	83	78	92	99	...	...	1	1	...	...	10	5	...	...	...	...	II_9
10	83	81	90	107	...	1	...	...	2	...	6	15	...	...	...	...	II_{10}
11	375	374	441	443	1	6	4	3	5	7	22	14	...	...	...	...	II_{11}
12	103	127	125	136	1	...	...	...	2	...	7	8	1	...	...	...	II_{12}
13	135	116	119	169	1	1	...	1	...	...	9	8	...	...	...	...	II_{13}
14	101	92	116	105	1	1	...	...	...	...	4	20	...	...	...	...	II_{15}
15	29	56	45	63	1	...	1	...	1	...	1	3	...	...	...	...	II_{18}
16	45	58	50	77	...	...	...	4	...	1	2	...	...	...	...	...	II_{19}
17	33	37	27	40	1	1	...	...	1	...	2	1	...	...	...	...	II_{24}
18	31	45	30	36	1	...	...	1	...	1	1	2	...	...	...	1	II_{25}
19	236	231	283	276	6	2	4	3	9	1	6	6	...	1	...	...	II_{27}
20	47	63	31	62	1	...	...	...	...	...	2	4	...	...	...	...	II_{30}
21	66	79	101	64	...	...	2	4	...	...	17	52	...	...	...	...	II_{31}
22	325	307	209	250	1	1	3	2	1	...	139	251	2	1	...	...	IV_4
23	286	184	233	321	6	2	5	3	2	2	197	191	1	1	...	1	IV_5
	2,734	2,744	2,773	3,008	22	45	30	33	43	21	478	644	4	8	0	2	

The relation of the classes to each other is evident from the following diagram (III) which represents (as before)

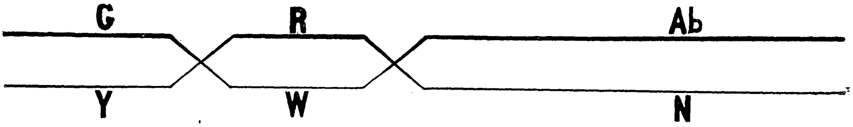

DIAGRAM III.

the sex chromosomes of the F_1 female. The classes of gametes of the F_1 females are the following:

Non-Crossovers	Single Crossovers	Double Crossovers
YWN	YRAb	YRN
RGAb	GWN	GWAb
	YWN	
	GRN	

In this and in the following tables the order of the cross-over gametes is always given the same, viz.: the first factor to the left above (Y) joins the two following below, R and Ab, (taking the switch as it were at the first cross-over). Then follows the cross-over that is the converse of the preceding (the first factor to the left below switching over to join W and N). The second crossing is taken in the same way, thus Y and W switch over to Ab, and conversely G and R switch over to N. The double cross-over takes the switch twice; thus Y to R and then to N; and conversely G to W and then to Ab. The F_2 flies should correspond to these gametic classes (since the F_1 male was a triple recessive) except in so far as the abnormal classes change to phenotypic normal types. Thus the non-cross-over class GRAb will, in this sense, contribute to the single cross-over class GRN; and the single cross-over class YRAb to the double cross-over class YRN. The last-named class can not, therefore, be used as a measure of the double crossing over, since it is more probable that any flies of this kind that appear will be only phenotypic YRN, than that they should belong to the YRN class genetically. Only the GWAb class may be used as a measure of double crossing over, and, as will be shown below, much caution must be used even in this case.

It will be seen in the table that only relatively few of the GRAb type have changed to the normal type, because the conditions were favorable for abnormal although the cultures ran in most cases for ten days, but during this time they still contained plenty of wet food. It will be noticed that the changed class GRN corresponds to one of the single cross-over classes, consequently GRN is a mixed class, and can not be used to base any calculation on. It is true, one may roughly determine how many cross-overs are expected in this mixed class by comparison with the other single cross-over class (YWAb). If these are subtracted, the remainder shows how many of this GRN class are due to a change from the abnormal to normal. Another point to note is that one of the double cross-over classes, viz., YRN, is likewise subject to addition from the single cross-over class, YRAb, and can not itself be taken as a measure of double crossing over, while, on the contrary, all cases in the other double cross-over class, viz., GWAb, count for their full value. Only two such double cross-overs occurred.

On the basis of the amount of single crossing over it is possible to calculate, as Sturtevant has shown, the expected number of double cross-overs. The number of the double cross-overs (two) in Table VIII is larger than expected. I repeated (December, 1913) the last experiment to test the question because abnormal arrangement of the rings of the abdomen is not a very rare occurrence and may sometimes be the result of injury to the larva or to the pupæ, or in still other cases may be due to other mutations, some of which will be described later. The abnormal mutation itself occurs not infrequently under conditions precluding contamination. In repeating the experiment extreme care was taken not to classify any fly

TABLE VIII

PARENTS: GRAb ♂ BY YWN ♀

F_1: GRAb ♀—YWN ♂

	YWN		GRAb		YRAb		GWN		YWAb		GRN		YRN		GWAb	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
A	58	64	57	56	0	0	0	0	5	0	0	1				
D	59	67	45	63	2	4	1	0	0	3	1	1				
E	72	90	60	76	0	1	0	2	0	1	2	3				
F	97	92	88	71	1	2	1	2	3	2	1	3				
H	31	41	47	58	1	0	0	0	0	0	3	3				
J	37	50	45	55	1	1	1	1	0	1	3	2				
K	64	65	56	52	2	0	1	0	2	0	1	2				
L	83	90	115	120	2	0	1	0	3	1	4	3				
M	64	65	74	75	0	2	0	0	3	3	6	3				
N	40	51	38	57	0	0	0	0	0	1	3	3				
Totals.	605	675	625	683	9	10	5	5	16	12	24	24	0	0	0	0

in the double cross-over class as abnormal unless there could be no reasonable doubt as to the nature of the character. In case of doubt the flies were tested by crossing again.

As before, yellow white normal (abdomen) females were crossed to gray red abnormal males. These gave in F_1 YWN ♂ and GRAb ♀ which inbred gave the results shown in Table VIII.

The double cross-over class is GWAb. The combination did not appear once amongst the 2,690 flies that are recorded in F_2. The percentage of crossing over between Y and W is 1.0; that between W and Ab was 2.1. The expectation of double crossing over on this basis (without interference) would be .02 per cent., or about 1 in 5,000. But the expectation would be far smaller than this because of a principle that we call interference. We mean by this term that should a cross-over occur at one point the chance of another occurring near it is greatly diminished, because if crossing over is due to twists of the chromosome the length of a twist would usually preclude the occurrence of two cross-overs near one another. In other words, if the loop that makes the twist is more likely to be of a certain length then the likelihood of the occurrence of a small loop necessary for a double cross-over is very small. In two cases, *B* and *C*, the F_2 counts (from pairs of F_1 flies) gave no YWN males as shown in the next counts.

	YWN		GRAb		YRAb		GWN		YWAb		GRN	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
B	0	55	51	41	1	1	0	0	0	2	1	3
C	0	49	47	47	0	1	0	0	0	2	0	4

The absence of the YWN males, when the other classes showed that no error in the experiment had been made, was not understood until the occurrence of lethal factors was worked out. Here clearly a lethal factor in the YWN grandmother has been carried over into her GRAb daughter. The lethal factor must have been closely linked with yellow and with white. The F_1 YWN son of the original YWN female must have come from the other sex chromosome of the YWN female—the one that did not carry the lethal. The count of the males in the F_2 gives both in *B* and in *C* a 2:1 ratio which is the characteristic ratio for a sex-linked lethal. The reciprocal cross was also made, but only twice; the F_2 counts are given in Table IX.

TABLE IX

PARENTS: GRAb ♀ BY YWN ♂
F_1: GRN ♀ (OR SLIGHTLY Ab)—GRAb ♂

YWN		GRAb		YRAb		GWN		YWAb		GRN		YRN		GWAb	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
141	...	165	339	...	...	2	...	1	...	59	110	...	...	...	...
202	...	225	562	3	...	...	...	7	...	10	11	...	...	1	...

The expected gametes of the F_1 female are the same, of course, as before, but the male contains all three sex-linked dominant factors, GRAb. Consequently in F_2 half of the GRAb female class is pure and half is heterozygous for abnormality. The GRAb F_2 males, on the other hand, are all pure, in the sense that they have only one factor for abnormal and no factor for normal. It is probable that most of them here are phenotypically abnormal.

The relation of the non-cross-over and the cross-over gametes is the same as in the reciprocal cross, since only sex-linked factors are involved, but the cross-over classes given in Table IX are different in the female classes in so far as the female producing sperms, that carry GRAb, contain three dominants. In one of the two counts given in the table the cross-over class that has changed to phenotypic normal is relatively large; in the other count it is small.

Gray, White, Abnormal by Yellow, Red, Normal

The next largest series of experiments involves the same three pairs of characters but combined in a different way. The results are shown in Table X. Diagram IV shows the relative positions of the factors in this combination.

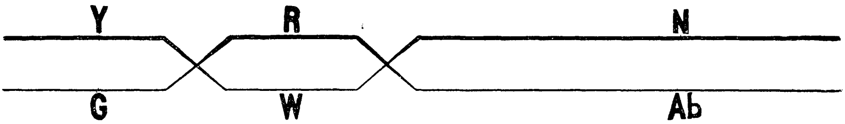

DIAGRAM IV.

The gametes produced by the F_1 female are the following.

Non-Crossover Gametes	Single Crossover Gametes	Double Crossover Gametes
YRN	YWAb	YWN
GWAb	GRN	GRAb
	YRAb	
	GWN	

The classes of special interest are non-cross-over GWAb males which change as the culture gets old into GWN (which is a single cross-over class), and GRN which is the corresponding female class (but heterozygous).

TABLE X

PARENTS: GWAb ♂ BY YRN ♀

F_1: GRAb ♀ (TO N)—YRN ♂

YRN		GWAb		YWAb		GRN		YRAb		GWN		YWN		GRAb		
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
3	42	32	...	...	...	...	2	45	1	3	...	...	...	...	67	III$_{3}$
470	494	329	...	1	...	10	185	1	...	115	...	1	...	...	232	III$_{20}$
92	101	99	...	...	...	...	.....	1	...	17	...	1	...	...	124	III$_{21}$
127	123	50	...	...	...	3	51	...	1	56	...	...	...	...	130	III$_{26}$
184	196	181	...	1	...	7	20	...	...	8	...	...	...	...	239	III$_{26}$
234	286	168	...	...	...	6	155	...	...	69	...	...	...	...	151	III$_{31}$
108	149	80	...	1	...	...	114	...	...	49	...	...	...	...	79	III$_{32}$
321	381	218	...	1	...	2	256	3	1	123	1	1	...	...	259	III$_{37}$
158	167	54	...	1	...	...	105	1	1	104	...	2	...	...	96	III$_{42}$
178	169	60	...	...	...	8	155	2	...	140	...	1	...	...	62	III$_{43}$
185	181	107	...	...	...	1	91	...	...	80	...	1	...	...	119	III$_{54}$
100	109	54	...	...	...	3	20	1	1	28	...	1	...	...	114	III$_{55}$
189	185	141	...	1	...	1	44	...	...	27	...	...	...	...	172	III$_{57}$
332	322	233	...	3	...	10	45	3	1	27	...	4	...	...	309	III$_{64}$
244	279	19	...	...	...	6	324	...	1	123	1	...	...	...	14	III$_{65}$
147	144	98	...	...	...	6	169	...	...	86	...	...	...	...	8	III$_{67}$
236	221	244	...	2	...	1	105	2	...	56	...	1	...	...	241	III$_{68}$
30	25	19	...	...	...	...	31	1	...	3	...	...	...	...	19	III$_{77}$
230	227	97	...	...	...	5	161	...	...	176	...	3	...	...	86	III$_{79}$
106	80	74	...	...	...	1	112	...	1	43	...	3	...	...	30	III$_{90}$
130	115	98	...	...	...	1	81	1	...	54	1	...	...	...	64	III$_{92}$
111	128	82	...	2	...	11	116	...	...	49	2	1	...	2	61	III$_{98}$
65	83	40	...	...	...	1	37	...	...	23	...	...	...	...	47	
225	202	100	...	...	...	2	142	...	...	93	...	...	...	...	94	
4,205	4,409	2,677	...	13	...	85	2,521	61	8	1,552	5	20	...	2	2,817	

An examination of Table VI shows how extensively changing took place in almost every one of the experiments. The contrast with the result of Table V is very striking.

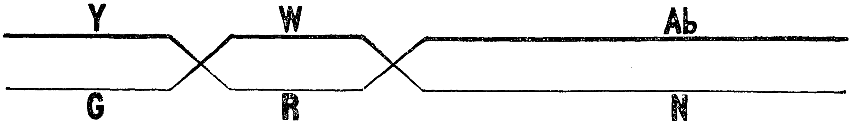

DIAGRAM V.

Yellow, White, Abnormal by Gray, Red, Normal

The experiment was made once one way (Table XI) and seven times reciprocally (Table XII). In the first case nearly all of the GRAb females are of the normal type. The only GR males that are abnormal are single cross-overs (Diagram V). This means that the heterozygous females are affected more easily than are the pure males;

TABLE XI

PARENTS: YWAb ♀ BY GRN ♂
F$_1$: GRN ♀—YWN ♂

GRAb		YWN		GWN		YRAb		GRN		YWAb		GWAb		YRN		
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
3	105	58	25	1	1	...	2	167	145	74	47	...	3	5	10	III$_{23}$

TABLE XII

PARENTS: YWAb ♂ BY GRN ♀
F$_1$: GRN ♀—GRN ♂

GRAb		YWN		GWN		YRAb		GRN		YWAb		GWAb		YRN		
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
		97	...	5	...	...	...	225	536	....	...	...	...	57	...	III$_{25}$
	25	15	...	...	...	...	...	205	313	28	...	...	...	4	...	III$_{29}$
1 slight	...	71	1	2	...	...	...	87	202	....	...	...	...	...	...	III$_{41}$
1	71	33	...	...	...	...	...	198	259	46	...	2	...	...	...	III$_{46}$
3	69	40	...	5	...	...	...	488	648	59	...	6	...	3	...	III$_{58}$
		47	...	2	...	...	...	67	113	....	...	...	...	1	...	III$_{78}$
1	9	5	...	1	...	...	...	219	249	36	...	1	...	1	...	III$_{91}$
Total 5.	174	308	1	15	...	...	...	1,489	2,320	169	...	9		66	...	......

---

[4] There is an exceptional case in the table, viz., two GWN ♀.

but even amongst the females a large percentage of gray reds are normal. The yellow white abnormal class is relatively much more abnormal, *i. e.,* relatively fewer have undergone the transition.

The results from the reciprocal cross are given in the next table. Here the F_1 male contains two dominants (GR) and one recessive factor (N). The females GRN YWAb carry only one dose of Ab, yet they are largely abnormal. The GRAb are single cross-overs.

Yellow, Red, Abnormal ♀ by Gray, White, Normal ♂

Only one experiment of this kind was made, but as the number of F_2 flies was rather large the results may be given (Table XIII).

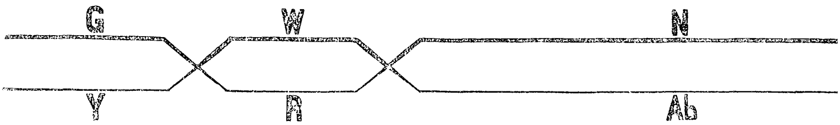

Diagram VI.

TABLE XIII

Parents: YRAb ♂ by GWN ♀

F_1: GRAb ♀—GWN ♂

GWN		YRAb		GRAb		YWN		GWAb		YRN		GRN		YWAb	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
166	171	135	....	....	154	....	....	2	1	....	....	1	36		
198	215	183	....	....	192	....	....	1	1	....	....	....	31		
210	215	179	....	....	232	2	....	1	1	....	....	....	85		
217	223	165	....	1	140	1	....	3	....	....	....	1	101		
791	824	662	....	....	718	3	....	7	3	....	....	2	253		

In this cross the gametes are as follows:

Non-Cross-over	Single Cross-over	Double Cross-over
GWN	GRAb	GRN
YRAb	YWN	YWAb
	GWAb	
	YRN	

The F_1 male is GWN and contains, therefore, one dominant sex-linked factor, viz., G. Therefore, all of the F_2

females are gray. The F_2 male classes alone can be used for testing the extent of crossing over.

CHANGE OF TYPE AS THE CULTURE GROWS OLDER

The preceding tables do not bring out the change that takes place as the culture gets older—a change by which the abnormal classes become replaced by the normal classes. A few results will therefore be given in detail to illustrate this relation.

In none of the relatively few counts in Tables I, and II, involving two pairs of factors (RN and WAb), was any change in type during the time of the experiment noticed; but in other cases a very marked change was observed as the cultures grew older.

In the two following tables consecutive counts of the F_2 flies (from YRAb ♂ by GWN ♀) emerging from day to day from the same culture are given. The change of the YRAb to the YRN and of GRAb to GRN is very striking.

TABLE XIV

PARENTS: YRAb ♂ BY GWN ♀
F_1: GRAb ♀—GWN ♂

	YRAb		GWN		YWN		GRAb		YRN		GWAb		YWAb		GRN	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
III_2....	81	...	98	88	....	....	...	95	1	...	1	1	...	...	1	....
	47	...	49	49	....	...	...	56	2	...	1	....	....	...	...	4
	7	...	19	34	....	...	...	3	25	...	....	....	...	...	...	32
	135		116	171	....	...	...	154	28	...	2	1	...	...	1	38
III_{74}...	57	...	44	55	1	...	...	83	....	...	....	1	...	...	...	....
	38	...	39	39	1	...	...	43	....	...	....	....	...	...	...	....
	44	...	33	38	....	...	...	64	....	...	1	....	...	...	...	....
	40	...	36	27	....	...	...	36	....	...	....	....	...	...	...	4
	....	...	63	51	....	...	...	6	74	...	....	....	...	...	...	81
	179	...	215	210	2	...	...	232	74	...	1	1	...	...	...	85

In the next table two F_2 counts are given derived from GWN ♀ by BRAb ♂ grandparents. The GRAb changes to GRN and BRAb to BRN.

TABLE XV

PARENTS: BRAb ♂ BY GWN ♀
F_1: GRN ♀ (OR SLIGHTLY Ab)—GWN ♂

Counts	GRAb		GRN		BRAb		BRN		GWAb		GWN		BWAb		BWN		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
1	23	33	0	13	5	5	0	0	...	...	23	26	...	...	3	6	III_5
2	6	16	0	11	2	3	2	4	...	...	13	9	...	...	2	2	
3	1	0	17	24	0	0	6	7	...	...	15	24	...	...	5	7	
4	0	0	36	40	0	0	15	12	...	...	41	39	...	...	15	22	
5	6	3	76	71	0	0	31	20	...	...	67	81	...	...	23	21	
1	19	24	1	0	11	6	2	0	...	...	23	20	...	...	10	8	III_{19}
2	26	28	0	0	7	10	0	0	...	...	50	29	1	...	9	12	
3	29	30	0	0	8	2	3	0	...	...	28	37	...	...	7	7	
4	8	13	2	0	6	5	0	0	...	...	11	14	...	...	4	4	
5	0	0	27	43	0	0	12	13	...	...	32	42	...	...	7	13	
6	0	0	36	51	0	0	17	16	...	...	51	49	...	...	10	21	

In the next case eight consecutive F_2 counts are given. The GRAb changes to GRN. In the first three counts there are 221 GRAb to 76 GRN, or 3 to 1. In the last three counts there are 148 GRAb to 296 GRN or 1 to 2.

TABLE XVI

PARENTS: GRAb ♂ BY YWN ♀
F_1: GRAb ♀—YWN ♂

YWN		GRAb		YRAb		GWN		YWAb		GRN		YRN		GWAb	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
105	90	91	100	0	0	1	1	0	0	15	51	1	1		
20	27	17	19	0	0	0	0	0	0	2	2	0	0		
32	35	33	51	0	0	1	0	0	0	2	4	0	0		
7	5	5	3	0	0	0	0	0	0	0	4	0	0		
5	4	1	1	0	0	0	0	0	0	3	11	0	0		
67	55	14	15	0	0	1	1	1	0	95	127	1	0		
47	28	23	22	0	0	0	0	0	0	18	36	0	0		
42	63	35	39	1	1	0	0	0	0	4	16	0	0		
325	307	219	250	1	1	2	2	1	0	139	251	2	1	0	0

Finally six cultures are given in the following table of F_2 flies from YRN ♀ by GWAb ♂ grandparents. The GWAb males change to GWN males and the GRAb females to GRN females. In both cases the increase in the normal flies in the last two or three counts is marked.

TABLE XVII

PARENTS: GWAb ♂ BY YRN ♀
F$_1$: GRAb ♀—YRN ♂

	YRN		GWAb		YWAb		GRN		YRAb		GWN		YWN		GRAb	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
III$_{20}$...	44	43	32	...	...	...	...	3	...	...	...	...	...	...	...	46
	36	53	33	...	...	...	...	...	1	...	1	...	...	...	...	73
	59	68	71	...	...	...	...	2	...	...	4	...	...	...	...	57
	72	67	56	...	...	...	2	...	...	...	7	...	...	...	...	35
	84	98	38	...	1	...	...	18	...	...	31	...	1	...	...	3
	25	15	20	...	...	...	1	10	...	...	9	...	...	...	...	3
	60	49	49	...	...	...	1	4	...	...	6	...	...	...	...	11
	37	40	28	...	...	...	1	17	...	...	17	...	...	...	...	3
	38	43	2	...	1	...	...	...	...	...	28	...	...	...	...	...
	15	18	...	...	...	...	1	15	...	...	12	...	...	...	...	...
III$_{31}$...	44	51	35	...	...	...	1	1	...	...	...	...	...	...	...	80
	36	43	28	...	...	...	1	...	...	...	...	...	...	...	...	44
	50	46	46	...	...	...	...	29	...	...	1	...	...	...	...	24
	29	48	6	...	...	...	...	42	...	...	36	...	...	...	...	...
	75	98	53	...	...	...	4	83	...	...	32	...	...	...	...	3
III$_{42}$...	28	33	21	...	1	...	...	...	...	1	...	...	...	...	...	46
	27	24	26	...	...	...	...	...	1	...	8	...	...	...	...	48
	42	38	2	...	...	...	...	50	...	...	40	...	...	...	...	2
	42	31	5	...	...	...	...	29	...	...	26	...	...	...	...	...
	19	44	...	...	...	...	...	26	...	...	30	...	2	...	...	...
III$_{43}$...	26	36	32	...	...	...	...	6	2	...	1	...	...	...	...	39
	25	22	28	...	...	...	...	47	...	...	55	...	...	...	...	19
	57	41	0	...	...	...	...	72	...	...	76	...	...	...	...	4
	63	68	0	...	...	...	...	7	...	...	8	...	1	...	...	...
	8	2	0	...	...	...	8	23	...	...	...	...	...	...	...	...
III$_{64}$...	39	21	29	...	...	...	2	...	...	...	...	...	...	...	...	...
	144	181	126	...	1	...	1	...	2	1	1	...	1	...	...	41
	97	94	78	...	2	...	5	3	1	...	3	...	1	...	...	187
	42	26	...	...	...	...	2	42	...	...	23	...	2	...	...	81
III$_{79}$...	46	39	47	...	...	...	...	10	...	...	1	...	...	...	...	65
	23	24	28	...	...	...	1	...	...	...	1	...	...	...	...	19
	18	12	17	...	...	...	...	16	...	...	4	...	...	...	...	1
	15	15	5	...	...	...	1	12	...	...	11	...	...	...	...	1
	32	39	...	...	...	...	4	44	...	...	56	...	1	...	...	...
	62	64	...	...	...	...	...	46	...	...	63	...	1	...	...	...
	34	34	...	...	...	...	1	33	...	...	40	...	1	...	...	...
	1,431	1,608	1,101	...	6	...	37	687	7	2	631	0	11	0	0	938

TESTS OF CHANGED-OVER CLASSES

In a number of cases in which some members of an abnormal class changed over to become phenotypically members of a normal class; some of these apparently normal flies were tested under conditions favorable for the appearance in the next generation of abnormality.

These cases may be given. Two kinds of crosses are expected. In a few cases the normal will be found to be a true normal (single cross-overs) and give therefore only normal offspring when bred to normal (recessive). In other cases the expectation is for abnormal offspring, and where change of type has been extensive, these kinds will be in the majority.

In experiment II_{12} one gray red normal female when tested gave GRAb ♂ and ♀.

In experiment I_1 seven GRN ♀ were bred to BWN ♂. Four gave some abnormal offspring and three gave only normal offspring.

In experiment I_3 five GRN ♀ were tested. Three gave some abnormal, two gave only normal offspring.

In experiment II_5 seven GRN ♀ were tested. Four gave some abnormal offspring, and three gave only normal offspring.

In experiment III_1 one GRN ♀ tested gave some abnormals.

In III_2 one GRN ♀ bred to YRN ♂ gave some GRAb ♂♂ and ♀♀.

In III_5 some BRN ♂ were bred to their BRN sisters. All BR offspring were abnormal.

In III_{11} GRN ♀ paired to GRN ♂ gave GRAb ♂ and ♀.

In III_{20} GRN ♀ bred to GWN brothers gave GRAb ♀ and GWAb ♂ and ♀.

In III_{35} GRN ♂ to GRN ♂ gave GRAb ♂ and ♀.

In III_{35} GRN ♀ by GWN ♂ gave GRAb ♀ and GWAb ♂ and ♀.

In III_{42} GRN ♀ by GWN ♂ gave GRAb ♀ and GWAb ♂ and ♀.

In III_{54} GRN ♀ (17) by GWN ♂ (4) gave the same results as the last.

In III_{58} GRN ♀ × YWAb ♂ gave GRAb ♂ and ♀.

In III_{68} GRN ♀ to GWN ♂ gave GRAb ♂ and ♀ and YWAb ♂ and ♀.

In III_{79} GRN ♀ to GWN ♂ gave GRAb ♀ and GWAb ♂ and ♀ in three different tests.

In III_{90} one GRN ♂ (the only one present) when tested gave GRAb ♂ and ♀ and GWAb ♂ and ♀.

In III_{113} GRN ♀ to GWN ♂ gave GWAb ♂ and ♀ and GRAb ♀.

These results show without any question that in the great majority of cases the phenotypic normal class (when abnormality is expected) is in reality made up largely (entirely, except for cross-overs according to expectation) of genotypically abnormal individuals. Their abnormality is shown by suitable breeding tests such as those here recorded.

INFLUENCE OF THE FACTOR FOR BLACK ON THE REALIZATION OF THE ABNORMAL CONDITION

Some of the evidence seemed at times to indicate that flies heterozygous in black are less likely to show the abnormal abdomen, but even if this is true it is still uncertain whether this might not be due to other conditions than those caused directly by the heterozygosity for black. It might be that the black stock contained other factors that influence the cross. Moreover since the number of eggs laid by a given kind of female determines how many larvæ will appear in a given time, and since the relation of the larvæ to the food is an important factor in the results, it seemed hazardous to put any emphasis on such results.

In order that the heterozygous flies might be reared under conditions that the control showed were favorable for development of the abnormal condition in homozygous forms, some black, red-eyed normal females were mated to gray, white-eyed abnormal males. After the females were fertilized they were put into a new bottle with some of the stock white-eyed females (fertilized). Some of the daughters were red- and some white-eyed; all of the latter were very abnormal, but the red-eyed females (heterozygous) were all normal through five counts. At the fifth count the white-eyed males that had been abnormal up to this time became normal. The result is in accord with many similar observations; for as conditions alter, the abnormal males first change to normal, then the heterozygous females, and lastly the homozygous females.

Several attempts were made to find out if, when the F_1 female, heterozygous for abnormal abdomen, is herself abnormal, her offspring are more likely to be abnormal than when she is normal. There is evidence everywhere throughout the tables to show that the condition of the mother has absolutely no effect on her offspring.

In December–January, 1914, the following experiments were made which are the converse, in one respect, of some of the preceding experiments since black abnormal females were used. The crosses are indicated below.

(1) Black, white, abnormal ♀ by gray, white, normal ♂.
(2) Gray, red, abnormal ♀ by gray, white, normal ♂.
(3) Black, white, abnormal ♀ by black, white, normal ♂.
(4) Gray, white, abnormal ♀ by black, white, normal ♂.

The F_1 females from (1) compared with (2) should show whether females heterozygous for black (and abnormal) are less abnormal than those pure for gray; provided, white and red eye make no difference in the development of abnormality. The F_1 female from (3) compared with (4) should reveal whether pure black heterozygous for abnormal are less abnormal than flies heterozygous for gray as well as abnormal.

The results need not be given in detail. It was found that the (F_1) daughters from (1) show the same degree of abnormality as those in (2). Hence heterozygosis in black need not have any influence on the realization of abnormality. The mothers were not, however, in the same bottles, but in different cultures kept as much alike as possible. To this extent the experiments are unsatisfactory. It was found that F_1 females from (3) were like those from (4), hence no evidence was found that the heterozygous type is more affected than the homozygous black. But here also the flies were reared in different bottles. In order to overcome this difference, some abnormal females that were heterozygous for black were bred to black normal males (both having white eyes).

The daughters were either heterozygous for black or pure black, likewise the sons. Hence, direct comparison could be made. The following protocol gives the results for four successive counts:

1.	Black ♀ quite abnormal.	Intermed. ♀ quite abnormal.
	Black ♂ quite abnormal.	Intermed. ♂ quite abnormal.
2.	Black ♀ quite abnormal.	Intermed. ♀ quite abnormal.
	Black ♂ quite abnormal.	Intermed. ♂ quite abnormal.
3.	Black ♀ fairly abnormal.	Intermed. ♀ fairly abnormal.
	Black ♂ very abnormal.	Intermed. ♂ very abnormal.
4.	Black ♀ none present.	Intermed. ♀ fairly abnormal.
	Black ♂ one quite, one fairly abn.	Intermed. ♂ quite abnormal.

The evidence shows no difference between the extent of development of abnormality in the homozygous black and heterozygous black females and males.

In another way an attempt was made to get light on the same question. Red black females were mated to white abnormal males; and, simultaneously, red gray females were mated to white abnormal males. The females were later put into the same bottle and their offspring reared together. All the daughters for four counts were normal. At the fifth count an attempt was made to separate the two classes of daughters, which is possible, because the offspring heterozygous for black are darker than the grays. The heterozygous pairs were normal or slightly abnormal while the pure grays appeared a little more abnormal; but the difference is hardly to be relied upon, since the abnormality is less striking in the black flies.

To test this possibilty some of the preceding experiments were carried to F_2, when pure abnormal grays, intermediate and pure abnormal blacks appear. The most abnormal grays were no more abnormal than the most abnormal blacks, which so far as it goes shows that the homozygous black flies themselves may be as abnormal as the grays under the same conditions and with the same ancestry.

INFLUENCE OF THE FACTOR FOR YELLOW IN THE REALIZATION OF THE ABNORMAL CONDITION

Experiments similar to those with black were made with yellow. Yellow, white-eyed normal flies were bred to gray, white-eyed abnormal. In ten tests, the F_1 females were abnormal in eight cases, and normal in two. It is not apparent that the yellow factor has any decided influence on the results.

In order to compare the females heterozygous in black and in yellow, and others also homozygous in both, the four following tests were made. By utilizing the red and the white eye colors it was possible to distinguish between the different classes of females. Previous experiments, described above, had made it highly probable, that no effects are produced by red and by white, but by making reciprocal crosses here this possible effect was more certainly eliminated. In all cases the females were mated separately for a few days to gray, white-eyed abnormal males to better ensure fertilization and were then brought together in one bottle.

(1)

YWN ♀ by GWAb ♂.
BRN ♀ by GWAb ♂.

1. GR ♀ Fairly Ab.
   GW ♀ Fairly Ab.
2. GR ♀ Like last.
   GW ♀ Like last.
3. GR ♀ Like last.
   GW ♀ Like last.

(2)

BWN ♀ by GWAb ♂.
YRN ♀ by GWAb ♂.

1. 3 GRN ♀.
   1 GWN ♀.
2. 12 GR slightly Ab ♀.
   3 GW slightly more Ab ♀.
3. 1 GRN ♀.
   8 GW slightly Ab ♀.
4. 4 GRN ♀.
   8 GWN ♀.
5. 1 GRN ♀.
   10 GWN ♀.
6. 2 GRN ♀.
   14 GWN ♀.

In (2) the females heterozygous in yellow were slightly more abnormal than those heterozygous in black or at least they gave such an impression.

(3)

BRN ♀ by GWAb ♂.
GWN ♀ by GWAb ♂.

1. GR slightly Ab ♀.
2. GRN or nearly N ♀.
   GW fairly Ab ♀.
3. 5 GRN and 4 GR quite Ab ♀.
   GW ♀ quite to fairly Ab.
4. 13 GRN ♀.
   16 GW quite to slightly Ab ♀.
5. 15 GRN ♀.
   9 GW fairly Ab to N ♀.
6. 6 GRN ♀.
   10 GWN ♀.

(4)

BWN ♀ by GWAb ♂.
GRN ♀ by GWAb ♂.

1. 5 GR slightly Ab ♀.
   2 GW nearly N ♀.
2. 14 GR fairly to slightly Ab ♀.
   6 GW nearly N ♀.
3. GR slightly Ab to N ♀.
4. 28 GRN ♀.
   3 GWN ♀.
5. 17 GRN ♀.
   2 GWN ♀.
6. 6 GRN ♀.

In (3) the females heterozygous in black were slightly more normal than the grays. In (4) there is hardly any difference, but so far as difference is noticeable the heterozygous type (GW) is again more nearly normal. This difference was even more apparent in a second culture from the same parents.

THE RELATIVE INFLUENCE OF THE EGG AND OF THE SPERM ON THE CONDITION OF THE HETEROZYGOTE

At the time when the F_1 generation began to hatch the extent of the abnormality in the females was noted. This was at the time when the flies were taken out to become the parents of the F_2 generation. The terms used were necessarily somewhat vague, but give a fairly accurate idea of the condition of the cultures as a whole. If most of the flies were distinctly abnormal this was indicated by Ab to N, if more of the flies were normal or nearly so but some were abnormal this was indicated by N to Ab. If the flies were normal in appearance this was indicated by N. The results for many of the cases recorded in the preceding tables are brought together in the next table.

The results are far from uniform, as was to be expected, but in most cases it will be noted that when the female was normal and the male abnormal, the daughters were frequently normal or nearly so, while in the reciprocal cross the tendency was in the opposite direction, *i. e.*, the daughters were more likely to be abnormal. These records were made at a time when no suspicion of such a relation was present in my mind. If these observations are to be trusted they mean that when abnormality comes in with the egg the heterozygous female is more likely to show abnormality than when the abnormality comes in with the sperm. Conversely the result may be stated in this way—when normality comes in from the egg the daughters are more likely to be normal than when the normality comes in from the sperm. In other words, we might extend this conclusion and state that the cytoplasm of the egg has an influence on the soma of the individual which arises from it, or the cytoplasm plus the nucleus of the egg has more influence on the next generation than the nucleus of the sperm.

	Abn.	Abn. to N.	N. to Abn.	N.
GWN ♀ YRAb ♂			2	3
YRAb ♀ GWN ♂				
YRN ♂ GWAB ♂	3	2	10	10
GWAb ♀ YRN ♂	3			
GRN ♀ YWAb ♂			1	7
YWAb ♀ GRN ♂				2 (few)
YWN ♀ GRAb ♂	14	2	6	1
GRAb ♀ YWN ♂			1	1
GWN ♀ BRAb ♂	3		3	4
YWN ♀ BRAb ♂				2
GWN ♀ GRAb ♂	4	1		1
GRAb ♀ GWN ♂	8			

When this possibility was realized it was evident that some of the experiments must be repeated under conditions where a more exact comparison between a cross and its reciprocal could be made. In the autumn of 1913 I went over the ground again with this object in view. It was found that the F_1 females heterozygous for abnormality are just as likely to be abnormal when their abnormal factor comes from the father as when it comes from the mother. The extent to which the abnormality is realized depends on the condition of the food. This in turn will depend in part not only on its amount but to what extent it is worked over by the larva which again depends, in large part, on the number of eggs laid by the female. To this extent and only in this sense does the condition of the mother affect the condition of her daughters. If the females lay too many eggs for the amount of food that is present, crowding results and the daughters show abnormality to a less degree than when fewer eggs are laid (that hatch) and little competition takes place. Now the normal female is more likely to lay more fertile eggs than the abnormal female. Hence other things being equal the heterozygous daughter of a normal mother is more likely to be normal than the heterozygous daughters of an abnormal female (which are therefore again more like their mother—very abnormal in this case, because the former mother is more likely to lay more eggs than the latter). The relation between the two cases is therefore not owing to the egg transmitting abnormality to the daughters better than the sperm, but to the number of eggs likely to be laid by the mother in question.

In order to examine further whether when abnormality comes in with the egg it is more likely to be shown in the F_1 heterozygote, a number of parallel experiments were made, of which the following are samples:

Gray Red Abn. ♀ by Wild ♂.	Gray Red Abn. ♂ by Wild ♀.
(1) Very abn. ♂ and ♀.	(1) Fairly abn. ♀.
(2) Normal (a few slightly abnormal).	(2) Most fairly, a few very abn.
(3) Normal (a few slightly abnormal).	(3) Most fairly, a few very abn.
(4) Normal (a few slightly abnormal).	(4) Slightly abn.
	(5) Slightly abn.
	(6) N ♀ (40) 1 slight abn. ♀.
	(7) N ♀.

While it is true in the first count above that when abnormality entered through the egg there was greater abnormality in the offspring, yet this is offset by the counter evidence in this set that the change to the usual phenotype took place sooner in this set than in the others. This point will be taken up again in connection with other data.

In order to compare, under changing conditions, heterozygous and homozygous females, some white abnormal females were mated to red abnormal males, and, independently, some other white abnormal females were mated to red normal males. After several days both kinds of females were separated from their respective males and put together into a single new bottle. All of the daughters had red eyes. In the first count two types of females could readily be distinguished. Some were quite abnormal, others were slightly abnormal or normal. In the second count (next day) again two types appeared, one quite abnormal and the other slightly abnormal females. In the third count some females were fairly abnormal, the rest normal and this held for the fourth count. The result leaves little doubt that under these conditions, the homozygous were abnormal and the heterozygous less abnormal or quite normal.

In order to see if the factors for red and for white affect the condition of the zygote, homozygous for abnormal; white abnormal females were mated to red abnormal males, and, separately, other white abnormal females to white abnormal males. After several days the females were put together in a new bottle and the males removed. Through five consecutive counts the red and the white daughters were alike, at first quite abnormal, later nearly normal. Red and white abnormal females therefore behave alike.

PRESENCE AND ABSENCE

It is not without interest to examine the bearing of these results from the point of view of the "presence and absence'' hypothesis, even although I myself prefer a more non-committal form of factorial interpretation than that offered by the ''presence and absence'' theory.

The abnormal male (Ab) has one dose of abnormality and the degree of his abnormality is the same as that of the female (Ab, Ab) with two doses. But the heterozygous female, AbN, has only one dose (or factor) for abnormality. The degree of abnormality that she shows is very variable; she is less abnormal on an average, than the abnormal male.

Which condition is to be interpreted as absence—the real absence of one Ab in the male, or the absence of one Ab in the other (normal) chromosome of the female? A moment's thought will show, however, that nothing of any value can come from a discussion of this question, because the heterozygous female (AbN) differs from the male not simply by the factor N, but by a whole chromosome including amongst other factors a factor which in duplex produces a female. Moreover, an advocate of presence and absence might maintain that the relation of a dominant to the normal allelomorph is not the same as the relation of a normal allelomorph to a recessive for it is the latter that is ''absent.'' In other words, he might conceivably accept the hypothesis of absence for a recessive, but reject it for a dominant mutation.

I have pointed out elsewhere that it seems to me unwarrantable to interpret the absence of a character to mean necessarily an absence of a factor in the germ plasm.[5] Yet this literal interpretation of the presence and absence hypothesis has often been made. If the linear arrangement of factors in the chromosomes be admitted as a plausible hypothesis the absence of a factor in this literal sense would mean a hole in the chromosome, and a corresponding displacement of the linear sequence of factors. The evidence does not support this hypothesis. On the other hand, if the locus of a factor be con-

[5] Although of course a changed factor might cause the failure of some substance to develop that is necessary for a given reaction.

ceived as a particular chemical body at a given level in the chromosome then any change in this body would be expected to affect one, or more, or even, at times, all characters of the complex that gives rise to the body character or characters. The particular change might involve no more than a rearrangement of the materials of the locus or the addition of a chemical element (or compound) or the loss of a chemical element (or compound) —any one of these changes might lead to the loss of a character in the soma. As to what happens in the locus we can form no idea, and so far as the mechanism of heredity is concerned it is a matter of no immediate importance. If, however, any one finds a greater satisfaction in the view that a loss of something from the locus (an atom or a molecule) leads to a recessive character, there is not the slightest objection to his doing so, unless by loss he means the loss of the entire locus. He may do this if he rejects the linear arrangement of different material in the chromosomes, but if he accepts the latter view the assumption of a literal absence involves him in unnecessary difficulties. It is not as generally understood as it should be that the facts which the presence and absence theory was constructed to account for do not require the assumption that the absence of a character means the absence of a factor in the germ-plasm. It is entirely gratuitous to involve the theory of Mendelian heredity in such an interpretation which adds nothing to the theory and by bringing in a new hypothesis may involve the Mendelian theory in further difficulties. An example may make this clear. It is known that when a chocolate mouse is bred to gray and the F_1 grays that result are bred together there appear in F_2 grays (9), cinnamons (3), blacks (3) and chocolate (1). Gray was written GBCh and chocolate gbC, which gave in F_2 GBCh (9) GbCh (3) gBCh (3) and gbCh (1). The occurrence of the black class of gBCh is accounted for through recombination. But the same end is accomplished if we suppose that a factor in the wild or agouti mouse mutated so that the recessive black was produced as a result of the activity of the new gene. Then bl = black, and Bl = gray with respect to black. Likewise cinnamon agouti may be represented by ci, and gray, with respect to cinnamon, by Ci. Chocolate is then the double recessive blci and the symbol Ch for "chocolate" becomes superfluous. All the experimental results may be explained on this basis.

It is not necessary to try to state what kind of a change in the germ-plasm led to these two mutations. The factorial hypothesis should be entirely non-committal as to the kind of change that took place, for we can know nothing about the nature of the change, yet the results are predictable as well on one view as on the other.

There is another way to interpret a dominant factor like this one that gives abnormality, namely, that there is present in the normal fly a factor that restricts the yellow of the abdomen to the bands. When this restrictor, ab, changes (Ab) the yellow is dispersed over the abdomen and the black bands fail in part or entirely to appear. The new factor, acting with the rest of the cell, gives abnormality, just as the normal restrictor or inhibitor (ab) acting with the rest of the cell gives normality or banding. The interpretation is non-committal in regard to the nature of the change, which is an advantage in the direction of simplification. In contrast to this view, a different interpretation of the meaning of a restrictor might be entertained on the presence and absence view. It might be said that a restrictor factor has been "lost" from the normal fly, which failing to restrict the color has given rise to abnormality. The first objection to this hypothesis is that it postulates (as above) the nature of the change in the germ plasm, because it says something has been lost. The second objection is that the facts show that a restrictor has not been lost *sensu strictu because there is a wide range of variation in regard to* *the loss of banding and in certain environments there is a return to the normal banding to the extent that the fly can not be distinguished somatically from a normal banded fly.*[6] My contention is that since we know nothing of the nature of the change in the germ-plasm that leads to the appearance of a new or the loss of an old character, any assumption that is based on the nature of that change involves the Mendelian interpretation in unnecessary implications. We need only assume that some change has occurred, as the result indicates; my formulas give the same results as do those of presence and absence and serve the purpose of briefly indicating a change, the machinery involved, and the necessary consequences.

OTHER TYPES OF ABNORMAL ABDOMEN

Irregularities in the arrangement of the rings of the abdomen are not uncommon in *Drosophila*. Sometimes they appear to have been caused by injury to the larvæ or pupæ, but still other abnormalities are inherited in the sense that they occur in certain stocks in more or less definite percentages. Several times I have bred abnormal types: some of them have failed to reappear; others have reappeared in a certain percentage of cases. Two stocks of the latter kind may be referred to here. My main purpose in describing them is to anticipate the possible confusion that might arise if some one finding these or similar ones should suppose them to be the same types as those described as abnormal abdomen in this paper.

The six drawings in Fig. 2, *a–f*, represent some of the characteristic types of a certain stock. The failure of the third abdominal ring to extend across the middle line, as

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[6] It is not an objection to this hypothesis that an absence (loss of restrictor) appears to dominate presence. This interpretation rests on a complete misunderstanding of the nature of the factorial hypothesis; for, absence here means only that the rest of the cell fails to produce banding when a certain factor is lost, or, when as in the female, one of the inhibitors is lost.

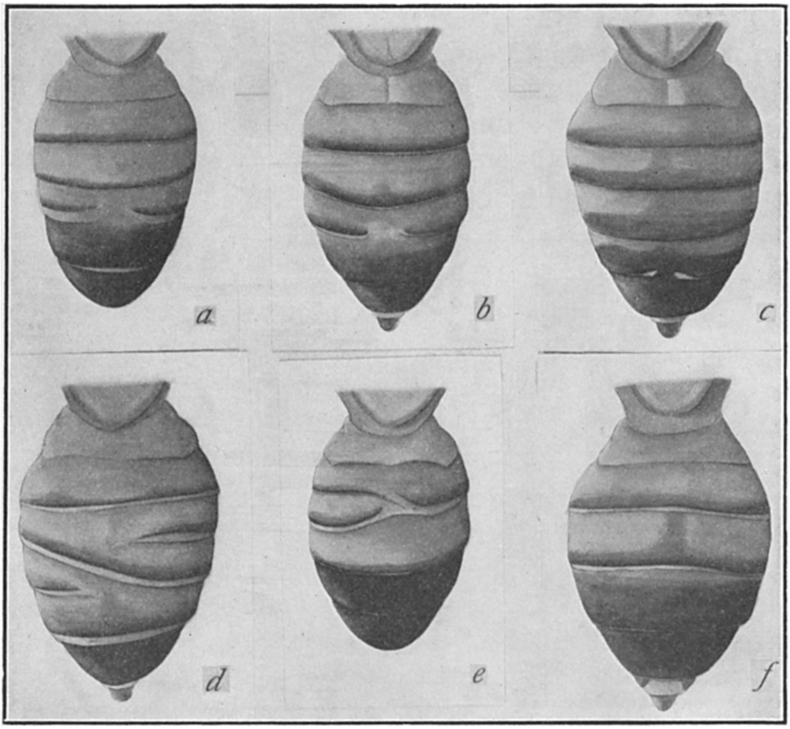

FIG. 2.

seen in the first two figures, is the more usual form of abnormality in this stock; but modifications of other rings shown in the other figures are probably due to the same cause or causes. Two consecutive rings may form a spiral as shown in *c* or half of a ring may be absent as in *e*, or an entire ring may be lacking as in *f*. Individuals with abnormalities like those shown in the figures were bred to each other usually three or four together. Their progeny was examined and the normal and the abnormal types recorded. The latter were again used to breed from for three or four generations. As no increase in the proportion of abnormal offspring appeared, the breeding was abandoned. The results given below are in the order in which they were obtained without regard to the generation in which they appeared.

In these counts there were normal to abnormal flies both of whose parents were abnormal. Since the normals also throw some abnormals it is probable that there is here a case of multiple factors like that of beaded and truncate. Special tests will therefore be necessary to work out the case.

N	Ab	N	Ab	N	Ab	N	Ab
85	7	43	13	40	0	73	0
6	1	13	2	18	1		
28	5	33	2	52	7	32	5
32	10	20	2	15	5	105	3
15	3	13	4	26	1	37	10
40	6	24	7	23	2		
31	6						

The abnormal abdomens shown in Fig. 3, *a–f*, are from another stock, discovered by Mr. Bridges. While some of the types are not unlike those of the last series, they are more extreme and there can be no doubt but that the two stocks have a different composition.

In the last drawing the entire fly is figured (the one wing present has been cut off at the base), the upper half of the thorax is absent. This same condition appears in rather high proportions in certain other stocks, notably in vestigial stocks. Even both sides of the thorax may be absent so that the head rests above on the abdomen. Although I have tried a number of times to obtain pure stocks of this thoracic abnormality, I have never succeeded in getting a stock that did not throw a high percentage of normal individuals.

This type of abnormal abdomen appeared in a cross between a cream male and an eosin female as a single female, Fig. 1, *a,* which had only three instead of five bands in the abdomen. She was mated to one of her brothers, and produced offspring all of which as far as known had normal bands. A pair of these offspring gave in the next generation abnormal bands in about half of the flies. The abnormal band acted as a recessive. In subsequent generations the character behaved in an irreg-

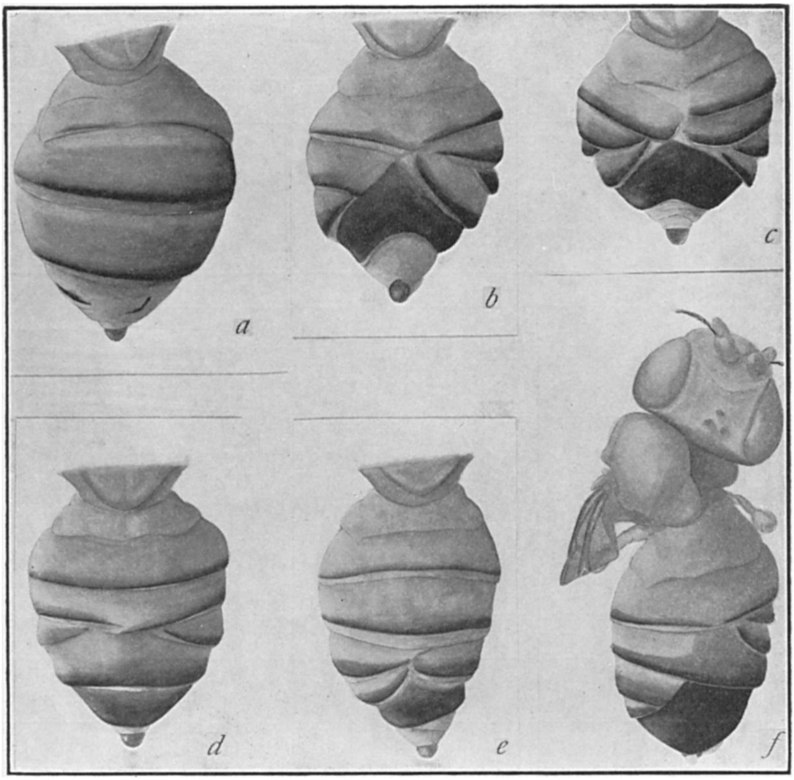

FIG. 3.

ular manner though no serious attempt was made to discover the cause of the irregularity. A stock of cream eye color was made up from this strain and selection against the abnormal was carried out in a rough way for several generations, but this selection failed to eliminate the abnormal condition, and a recent examination of the stock showed that for a year the abnormal abdomen had maintained itself and was still present in about half of the flies.

A male was again crossed to a wild type female and gave normal F_1 flies. In F_2 there were 128 red normal females, 29 red normal males, and 28 eosin normal males. No abnormals appeared. Crossed to eosin the F_1 were

PARENTS: AbE BY NE
F$_1$: NE

EN ♀	EN ♂	EAb ♀	EAb ♂
78	56	1	1
13	14	0	2
46	40	0	2
6	7	0	0
35	32	0	1
39	46	7	1
217	195	8	7

all normal; these inbred gave in F$_2$ the classes given above: Two eosin females heterozygous for white were crossed each to an abnormal male. The normal F$_1$ daughters were bred to those sons that had white eyes, and gave the following kinds of offspring:

PARENTS: E–WN ♀ BY EAb ♂
F$_1$: EN ♀ (BY WN ♂)

EN ♀	EN ♂	EAb ♀	EAb ♂	WN ♀	WN ♂	WAb ♀	WAb ♂
18	26	1	1	20	15	1	1
34	28	1	2	18	25	2	1
52	54	2	3	38	40	3	2

Abnormal males were bred to eosin females and gave, as before, normal F$_1$ sons and daughters. Some of the daughters were backcrossed to eosin cream abnormal males and gave the following results:

PARENTS: AbE BY NE
F$_1$: NE (BY AbE ♂)

EN ♀	EN ♂	EAb ♀	EAb ♂
35	32	0	1
21	4	1	2
48	40	0	1
72	72	8	6
176	149	9	10

These tables show that the abnormal condition rarely appears in F$_2$. Its realization must be due therefore either to multiple factors or to environmental effects. That the former rather than the latter is the main explanation is shown in the frequency with which the abnormal flies appear in the inbred stock (where the conditions are the same as in the experiments) and the rarity with which the character appears when the stock is outcrossed.

THE NON-INHERITANCE OF AN ACQUIRED CHARACTER

The acquirement of a new character by a pure stock implies by definition the capacity of this stock to respond to the imposed conditions. Conversely if an animal does not acquire a new character in a changed environment it does not come within the scope of the definition of an acquired character, and even should its offspring show new characters as a result of the new environment in which the parents have been placed the result is still excluded by definition from being a case of the inheritance of an acquired character. At least this is my understanding of the use of the term and the way in which I shall use it in the following statement.

The mutant stock of abnormal abdomen offers an exceptional opportunity to examine the possible influence of an acquired character on the offspring. As the experiments have shown this stock is very susceptible to environmental influence, and the effects produced profoundly affect the structure of the organism. Moreover it is possible to carry the stock through several generations in either of the phenotypic conditions, and then, at will, to cause the other type to appear at once in its completest form, by regulating the external conditions in which the young are reared.

No better material could be found for studying the possible influence of the environment through its effects on the soma of the individual. *The evidence shows in the clearest manner that the condition of the parent, whether normal or abnormal in type, has no effect on the character of the offspring.* The evidence is so clear and so positive that it seems unnecessary to elaborate the point.

THE NON-CONTAMINATION OF GENES

Recently the question of the possible contamination of genes (or factors) has been under discussion. Were such contamination possible one might expect to find some evidence of it in a case like this one of abnormal abdomen, if one is justified, at all, in drawing inferences from the nature of the character to the nature of the gene that stands for that character. I do not myself think that there is the slightest justification in drawing such conclusions, but let us assume for the moment that such an inference is justifiable in order to examine the bearing of the evidence furnished by this mutant type.

The heterozygous female carries a factor for normal and one for abnormal. She herself may be either normal or abnormal according to the environment in which she was reared. It might be supposed, since she is abnormal, that her normal gene might be more predisposed to contamination by the abnormal gene. The evidence shows that this does not occur; for, by means of the linkage we can identify the normal flies that should carry the normal, or the abnormal genes, and we find that the results conform completely to expectation; *i. e.,* they are in full accord with all other linkage results where there is no reason to suppose that contamination takes place.

Conversely it might be supposed that if the heterozygous female were normal in type her abnormal gene might be predisposed to contamination by the normal gene, but again the evidence contradicts the assumption.

If, on the other hand, it is *not* supposed that the phenotypic condition of the female has any part in bringing about contamination (or in serving as an indicator, that conditions are favorable for contamination) but that contamination is due merely to juxtaposition of genes in the same cell, then in refutation of the contamination of genes I may cite the evidence cited above, where in several successive generations the breeding took place from heterozygous females bred to recessive males and the gametic ratios were the same in the late as in the earlier generations.

Lastly the tests made of individuals that were phenotypically normal, but genetically abnormal, showed in all cases the validity of the genetic evidence, which would not have been the case if the apparent exceptions had been due to contamination of the genes. I may also cite the two peculiar matings, *B* and *C*, recorded on page 402, where an expected class did not appear. It might have appeared that here actual contamination had occurred. In reality, the result turned out to be due to a lethal factor. Our study of these lethals, that give verifiable results, fully under control, made it possible to interpret this case that otherwise would have been inexplicable, and might have been cited in favor of the view of contamination of genes. Taken all together the results obtained with this mutant type make out a strong case against the supposition that genes become contaminated through juxtaposition. I shall not discuss here, therefore, the unpragmatic character of such a supposition, but rest the case on the evidence from the experiments.